

THE PARASITIC BEHAVIOR OF THE BRONZED COWBIRD IN SOUTH TEXAS¹

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Abstract. Aspects of the breeding ecology of the Bronzed Cowbird (*Molothrus aeneus*) were studied from early April to mid-July or August 1980 to 1982 at the Santa Ana National Wildlife Refuge in southern Texas.

Female Bronzed Cowbirds, similar to Brown-headed (*M. ater*) and Shiny (*M. bonariensis*) cowbirds, are generalists in their egg laying. Of five common host species on the refuge, all were equally and usually repeatedly parasitized. Of these, only the Green Jay (*Cyanocorax yncas*) and Long-billed Thrasher (*Toxostoma longirostre*) are larger than the cowbirds in body size and are better host choices based on their relative success as fosterers. Experimental parasitism of Couch's Kingbirds (*Tyrannus melancholicus*), Curve-billed Thrashers (*Toxostoma curvirostre*), and Great-tailed Grackles (*Quiscalus mexicanus*) showed that they eject cowbird eggs from the nest.

Female Bronzed Cowbirds, like Shiny Cowbirds, pierce both host eggs and previously laid cowbird eggs. Approximately twice as many host eggs were pierced compared to cowbird eggs. In some parasitized nests, more than one cowbird laid eggs and final host clutch size was greatly reduced.

The vocal reaction of host species to cowbird intrusion probably provided clues on nest location to nest-searching female cowbirds who were drawn to such stimuli.

Like the other four parasitic cowbird species, Bronzed Cowbird nestlings possess no apparent special adaptation for brood parasitism. Their vocal nature, however, appears to give them a competitive edge against less vocal host nestmates.

Key words: Cowbird; Bronzed Cowbird; *Molothrus aeneus*; host specificity; social parasitism; brood parasitism; parasitic behavior.

INTRODUCTION

The Bronzed Cowbird (*Molothrus aeneus*) is one of four parasitic species in the genus *Molothrus*. Few facts have been published about the breeding biology of the Bronzed Cowbird, and it is the least known member of its genus. Early reports about its host-specific egg-laying habits led Friedmann (1929, 1963) to speculate on the phylogeny of the genus *Molothrus* and on the evolution of the parasitic habit. However, the evolution of the cowbird group remains unclear, and recent evidence indicates that the Bronzed Cowbird is more of a generalist than a host-specific parasite. Although Friedmann (1929) stated that the Bronzed Cowbird preferentially parasitized orioles, the current host list includes 72 species (Friedmann et al. 1977, Rowley 1984, Carter 1984).

Although female Bronzed Cowbirds are known to pierce host eggs (Friedmann 1929, Kiff cited by Mason 1980) and have been seen traveling in groups apparently searching for nests (Merrill 1877, Pleasants 1981), the incidence of these presumed adaptations has not been studied in detail. This paper describes the parasitic behavior of Bronzed Cowbirds, the behavioral adaptations of adults and juveniles for parasitism, the ability of foster species to

raise the parasites' young, and counter-adaptations of host species against parasitism.

This study was conducted in south Texas, where Bronzed and Brown-headed cowbirds (*M. ater*) are sympatric (Fig. 1) and both have extended breeding seasons (Oberholser 1974). The Brown-headed Cowbird is resident in Texas, but the Bronzed Cowbird, is "locally and erratically common to very rare through south Texas" in winter (Oberholser 1974:843) and its migratory habits are not known. Neither species is present during the winter on the study area, but they both arrive at about the same time in spring (mid-April) after dispersing from large mixed-species flocks.

Despite selection pressures resulting from inappropriate host choice, egg placement by molothrine cowbirds has been described as indiscriminate (Friedmann 1929, 1963; Rothstein 1976; Friedmann et al. 1977; Mason 1980). If true, how can this indiscriminate behavior be maintained by natural selection if some hosts foster better than others? To identify the better host choices for the Bronzed Cowbirds, I evaluated the relative success of all hosts in raising young Bronzed Cowbirds by noting the species seen feeding each cowbird fledging still begging for food.

Indiscriminate egg laying by brood parasites has obvious costs related to egg production. For this behavior to persist, there must be advantages that more than compensate for those

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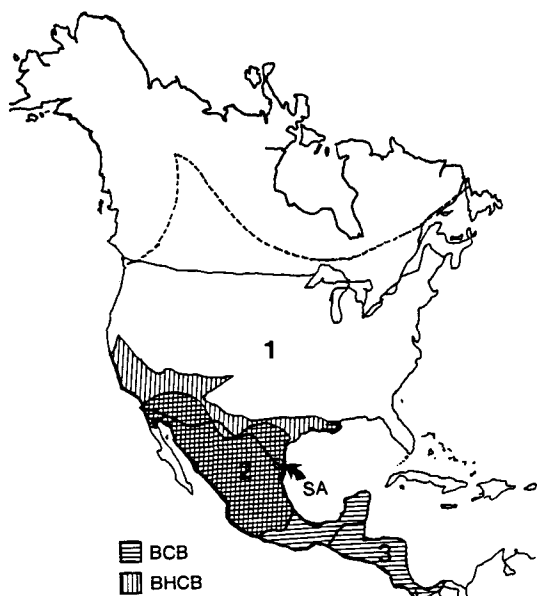


FIGURE 1. Ranges (shaded areas) of the Bronzed (BCB) and sympatric race of the Brown-headed Cowbird (BHCB) in the United States (1), Mexico (2), and Central America (3; AOU Committee 1983), plus the northern range limit (dotted line) of the latter cowbird species. The study site (SA) is at the tip of the arrow.

costs. By revealing the egg-laying pattern of the Bronzed Cowbird and the ecological context of that behavior, it should be possible to identify some of the selection pressures favoring the apparent indiscriminate egg placement by the Bronzed Cowbird and other generalist parasites and the evolution of the parasitic habit.

THE STUDY SITES

I conducted this investigation with the help of four field assistants on the Santa Ana National Wildlife Refuge (SANWR), Anzel Dua Tract of the Rio Grande Valley National Wildlife Refuge, Pharr, Texas, and the Countryside Trailer Park, Donna, Hidalgo County, Texas (26°15'31", 98°7'15") from the first week in April to mid-July of 1980 through 1982.

The SANWR is subtropical habitat along the Rio Grande, 12.1 km south of Alamo, Texas, and 72.4 km west-northwest of Brownsville, Texas. The 800-ha SANWR contains semi-arid forest, brushland, and mesquite-cactus associations; it receives an average annual rainfall of about 58 cm, much of which falls during the hurricane season in September and October. The land surrounding the refuge has been cleared for agriculture, leaving the refuge as a discrete island of natural vegetation. Of the widely scattered vegetation island remnants in the lower Rio Grande Valley that have been purchased or preserved by the U.S. Fish and Wildlife Service (USFWS), the SANWR

is one of the largest. Many of the breeding bird species endemic to southernmost Texas and northern Mexico are concentrated on (or restricted to) these small, scattered natural areas.

In order to identify the habitats comprising the SANWR, I examined aerial photos and made field observations during the 1980 season. I defined six habitat types (excluding open water) based on the gross structure of their vegetation:

Chaparral: brush and small trees, a few scattered large trees with canopy <10%; 42.5 ha; *Celtis pallida*, *Acacia rigidula*, *Porlieria angustifolia*, *Amyris texana*, *Xanthoxylum fagara*, *Pithecellobium flexicaule*, *Condalia hookeri*, *Ziziphus obtusifolia*, *Diospyros texana*, *Forestiera angustifolia*, *Leucophyllum frutescens*, *Castela texana*.

Thicket: dense shrub understory, tree canopy >10%; 326.2 ha; *Ulmus crassifolia*, *Acacia smallii*, *A. wrightii*, *A. greggii*, *Leucaena pulverulenta*, *Pithecellobium flexicaule*, *Ziziphus obtusifolia*, *Diospyros texana*, *Forestiera angustifolia*, *Ehretia anacua*, plus vines including *Smilax bona-nox* and *Mimosa malacophylla*.

Riparian Forest: forest with little understory, adjacent to the Rio Grande; 47.0 ha; *Salix interior*, *S. nigra*, *Celtis laevigata*, *Leucaena pulverulenta*, *Sapindus saponaria*, *Fraxinus berlandieriana*.

Mesquite-Cactus Association: 174.1 ha; *Acacia smallii*, *Mimosa pigra*, *Parkinsonia aculeata*, *Prosopis glandulosa*.

Old Field/Grassy Marsh Edge: 46.8 ha; in addition to grasses, *Mimosa pigra* was common.

Open Forest: little shrub understory, canopy cover nearly 100%; 113.3 ha; *Celtis laevigata*, *Ulmus crassifolia*, *Leucaena pulverulenta*, *Fraxinus berlandieriana*.

The extent of each habitat type (Fig. 2) was estimated by tracing the aerial photos on graph paper. The dominant woody plant species in each type were identified by field traverses.

Additional data on host nests were gathered on a 10-ha area of Anzel Dua, a satellite refuge tract near Pharr, about 20 km west of the SANWR and the Countryside Trailer Park in Donna, one ha in size and about 13 km north of the SANWR. The former area consisted primarily of cactus-mesquite associations. The trailer park was residential, with scattered fruit trees and shade trees surrounded by lawn.

METHODS

GENERAL

Ethological data were gathered on a 5-ha study plot in chaparral habitat in the northwest quar-

ter of the refuge. My field assistants and I spent 1,272 hr trapping cowbirds and observing their behavior. Cowbirds were captured in Potter and decoy traps (modeled after that in USFWS Pub AC 211) on the western edge of the refuge, and in mist nests on the study plot. Up to three decoy traps, each measuring 2 m on a side, were used simultaneously. Nets were open from sunrise until as late as 1500 six to seven days per week, resulting in a three-season total of 14,458 mist net hours. Captured females received a colored plastic band and a USFWS aluminum band on the left tarsus and two colored plastic bands on the right leg. Males received an additional plastic band above the aluminum band on the left tarsus.

BREEDING BIRD CENSUSES

We recorded 53 species breeding on the SANWR from 1980 through 1982. In 1981, three strip censuses were conducted at weekly intervals between 27 May and 9 June on 2.4-km transects in each of the six habitat types at the SANWR. Each census began at 0645 and ended before 1045. I used the methods of Balph et al. (1977) to estimate breeding bird densities from the detection data in each habitat type. The estimates (birds/ha) were used to calculate breeding pairs per 100 ha on the study site (Table 1) based on the amount of each habitat type present on the refuge (Fig. 2). Excluded from Table 1 are 17 non-passerine species that bred on the study site but were not detected during early morning censuses. In addition, we did not census Chachalacas (*Ortalis vetula*), White-winged Doves (*Zenaida asiatica*), Mourning Doves (*Z. macroura*), Ground Doves (*Columbigallina passerina*), Inca Doves (*Scardafella inca*), White-fronted Doves (*Leptotila verreauxi*), or Great-tailed Grackles (*Quiscalus mexicanus*) because of difficulties in estimating their numbers based on sounds. Although Mourning Doves (Friedmann 1971) and Ground Doves (Friedmann 1963) have been reported as Brown-headed Cowbird hosts, and White-winged Doves have been parasitized by Bronzed Cowbirds (Friedmann 1963), such events are very rare and are of little consequence to this study.

Seven common piciform and passerine species that breed on the SANWR may be inaccessible to cowbirds because they build domed nests (Verdin, *Auriparus flaviceps*; Cactus Wren, *Campylorhynchus brunneicapillus*; Great Kiskadee, *Pitangus sulphuratus*) or because they nest in cavities (Brown-crested Flycatcher, *Myiarchus tyrannulus*; Tufted Titmouse, *Parus atricristatus*; Golden-fronted Woodpecker, *Centurus aurifrons*; Ladder-backed Woodpecker, *Dendrocopos scalaris*).

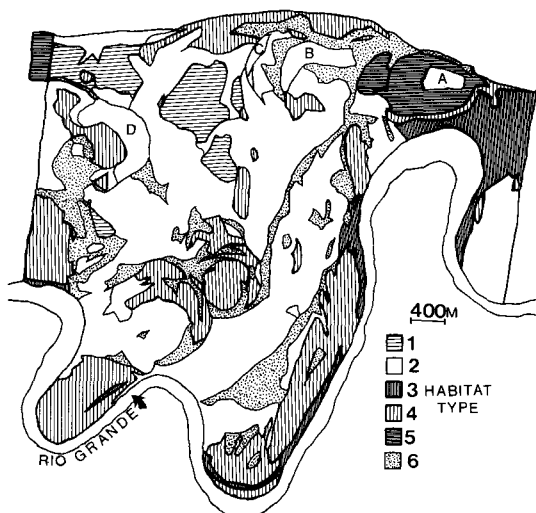


FIGURE 2. Habitat types on the Santa Ana National Wildlife Refuge (1-6) plus open water (A-D): (1) Chaparral; (2) Thicket; (3) Riparian Forest; (4) Mesquite-Cactus Association; (5) Old Field/Grassy Marsh Edge; (6) Open Forest.

The Yellow-billed Cuckoo (*Coccyzus americanus*) and Groove-billed Ani (*Crotophaga sulcirostris*), both common at the site, are also not used as hosts.

COWBIRD EGG DISTRIBUTION AMONG HOSTS

We searched for nests over much of the refuge from May to July in 1980 and 1981 between 0700 and 2000, six to seven days per week. In addition, in May and June 1980 three of us searched for nests for 36 hr at the Anzel Dua tract and at the Countryside Trailer Park. We noted the number of eggs (host and parasite) and young in each nest. The young (see Friedmann 1929 for description) and the unmarked pale blue eggs of the cowbird were easily distinguished from those of other species. We inspected nests at heights of 2 to 4 m by using a mirror on a telescoping pole, and nests above 4 m were examined by climbing to them. Particular attention was paid to oriole nests. At each, I observed and listened for oriole-cowbird interactions for at least 15 min at various times during the nesting cycle.

The occurrence of cowbirds piercing eggs was documented by visits on consecutive days to selected easily observable nests. To my knowledge, human visitation caused no desertions.

EXPERIMENTAL EGG MANIPULATIONS

I placed one real Bronzed Cowbird egg per nest in four nests of each of three species that were not parasitized (Couch's Kingbird, *Tyrannus melancholicus*; Curved-billed Thrasher, *Toxostoma curvirostre*; and Great-tailed Grackle) to determine if the hosts would eject foreign

TABLE 1. Average numbers of birds per hectare by habitat type (1-6) and the total (pairs per 100 ha) for species censused at the Santa Ana National Wildlife Refuge, indicating which species have hosted Bronzed (B) and/or Brown-headed cowbirds' (C) eggs, and which have raised (*) cowbirds.

Bird species	Average abundance (birds/hectare) by habitat						Breeding pairs/100 hectares
	1	2	3	4	5	6	
<i>Elanus leucurus</i>	0.16			0.16	0.18		3
<i>Parabuteo unicinctus</i>				0.08			1
<i>Colinus virginianus</i>	0.14		0.01		0.20		1
<i>Buorides virescens</i>		0.07			0.04		2
<i>Himantopus mexicanus</i>					0.43		1
<i>Charadrius vociferus</i> (C)					0.43		1
<i>Coccyzus americanus</i> (C)	1.25	1.20	0.66	0.93	0.04	0.54	44
<i>Crotophaga sulcirostris</i>	0.72	0.60	0.81	0.08	0.43	0.04	19
<i>Centurus aurifrons</i>		1.24	0.41	0.58		0.63	37
<i>Dendrocopos scalaris</i>		0.09	0.23			0.02	3
<i>Tyrannus melancholicus</i> (B*)	0.49	1.54	0.95			0.06	34
<i>Pitangus sulphuratus</i> (B)?	0.07	0.50	0.07	0.58		0.04	17
<i>Myiarchus tyrannulus</i>	1.26	1.65		0.93		1.06	52
<i>Eremophila alpestris</i> (C)					0.12		0.4
<i>Cyanocorax yncas</i> (B*)	0.74	0.65	0.34	0.13	0.02	1.60	29
<i>Parus atricristatus</i>	0.10	0.25	0.95	0.20		0.76	16
<i>Auriparus flaviceps</i> (C*)	0.22						1
<i>Campylorhynchus brunneicapillus</i>			0.05	0.05			1
<i>Mimus polyglottos</i> (B*, C)	2.30			0.13			8
<i>Toxostoma longirostre</i> (B*, C)	1.60	3.56					77
<i>T. curvirostre</i> (C)	1.51		0.06	0.31			8
<i>Vireo griseus</i> (C*)	0.05	0.50	0.09				11
<i>Passer domesticus</i> (C*)						0.02	0.1
<i>Agelaius phoeniceus</i> (B*, C*)	0.43				0.46		3
<i>Icterus gularis</i> (B)		0.06	0.21			0.06	2
<i>Molothrus ater</i>	0.14		0.14			0.01	1
<i>Molothrus aeneus</i>	3.21	3.25	0.14	0.47	4.29	0.49	96
<i>Cardinalis cardinalis</i> (B*, C*)	0.22	0.46					10
<i>Pyrhuloxia sinuata</i> (B, C)		0.03					1
<i>Arremonops rufivirgata</i> (B*, C*)	2.20	4.00		1.04	0.11		99

eggs. I added the eggs to two of the experimental nests of each species *before* and to the other two nests *after* the victims' clutches were complete. All eggs were added before 1200, and no host eggs were removed. An assistant or I visited each experimental nest once every 24 hr. Ejections were assumed to have occurred if the cowbird egg was missing while the host's eggs were still present.

FLEDGLING CENSUSES

I censused food-begging fledging cowbirds and their foster parents in June and July 1981 along the breeding bird census transects between 0700 and 2000 once along each transect. In 1982 similar censuses were performed with the help of two assistants, which nearly doubled the census hours that year.

NESTLING GROWTH RATES

In 1980 known-age cowbird nestlings being raised by five foster species (Couch's Kingbird; Green Jay, *Cyanocorax yncas*; Northern Mockingbird, *Mimus polyglottos*; Long-billed Thrasher, *Toxostoma longirostre*; and Northern Cardinal, *Cardinalis cardinalis*) were weighed (using 100-g Pesola spring scale ± 0.5

g) at about the same time (± 2 hr) every day. I determined the sex of nestlings based on their weights by the tenth day after hatching. To verify this method of identifying the sex of hatching-year cowbirds based on size/weight dimorphism, I dissected and examined the gonads of nestlings, fledglings, and juveniles. Additionally, I used information from recaptured individuals that had been banded in the nest. From May to July in 1981, we measured growth rates of nestlings of three host species (thrashers, mockingbirds, and cardinals) for comparison to the cowbird's growth rate. The rate constant (K , Ricklefs 1967), proportional to the overall growth rate, was used to compare rates of growth among species. Day 0 designates the day of hatching. Measurements were continued until nestlings died or fledged.

DIET OF HATCHING-YEAR COWBIRDS

I determined the diets of hatching-year (HY) cowbirds by examining the stomach contents of 12 nestlings, 72 fledglings (being raised by Green Jays; Long-billed Thrashers; and Olive Sparrows, *Arremonops rufivirgata*), and 16 juveniles. Stomachs were removed and frozen for later analysis at the laboratory to determine

TABLE 2. Adult Bronzed Cowbird rate of capture in mist nets in chaparral habitat, comparing eight one-week periods from May 13 to July 8 of 1980 and 1981, with numbers caught standardized to birds per 100 net-hours (NH).

	May		June				July		Totals
	13-19	20-26	27-2	3-10	11-17	18-24	25-1	2-8	
1980:									
Net hours (NH)	418	525	396	290	180	312	290	223	2,634
No. caught/100 NH	2.6	1.7	1.0	0.7	0.6	0.6	0.3	0.9	$\bar{x} = 1.1$
Total caught	11	9	4	2	1	2	1	2	32
1981:									
Net hours (NH)	678	542	558	737	338	632	338	258	4,081
No. caught/100 NH	0.9	1.3	0.4	0.3	0	0	0	0.4	$\bar{x} = 0.4$
Total caught	6	7	2	2	0	0	0	1	18

Wilcoxon's signed-ranks test, $P = 0.008$.

Ratio of average rate of capture (birds/net hour) 1980:1981 is 2.75:1.

the aggregate percent of total volume occupied by identifiable food items (Swanson et al. 1974). Final values for each food item were averaged over all individuals.

RESULTS

BIRDS BREEDING AT THE SANWR

Bronzed Cowbirds were nearly as abundant at the SANWR as the most numerous host species, the Olive Sparrow, and only slightly more common than the second most abundant host species, the Long-billed Thrasher (Table 1). The cowbirds outnumbered the jays by about 3 to 1. Mockingbirds, Red-winged Blackbirds (*Agelaius phoeniceus*), and cardinals were rare compared to the numbers of the parasite and other hosts. Assuming that they did not become net wary, cowbirds appeared to be more abundant in 1980 than 1981. The rate of mist-net capture of adult cowbirds (an indicator of abundance) in 1980 was higher (Wilcoxon's signed-rank test, $P = 0.008$) than during the same eight-week period in 1981 (Table 2).

COWBIRD-HOST SYNCHRONY

The cowbirds arrived at the SANWR in mid-April and began laying eggs by the first week of May in all three years. In contrast, egg laying by some hosts was earlier in 1981 relative to the previous year, correlating with differences in rainfall between the two years. In 1981, a year of more rainfall during March through July compared to the previous year, mid- to late-April clutches by Green Jays ($n = 1$), Long-billed Thrashers ($n = 2$), Northern Mockingbirds ($n = 2$), and Olive Sparrows ($n = 1$) escaped parasitism at the study site because they were laid before the cowbirds arrived.

BRONZED COWBIRD EGG DISTRIBUTION AMONG HOSTS

The distribution of cowbird eggs and young did not differ significantly among 48 nests of

six host species found in 1980 (Kruskal-Wallis one-way ANOVA, $P = 0.118$; Table 3). In that year, parasitism of the regular hosts (Green Jay, Long-billed Thrashers, mockingbirds, Red-winged Blackbirds, cardinals, and Olive Sparrows) was intense (100%). In 1981, however, mockingbirds were relatively less parasitized (Kruskal-Wallis one-way ANOVA, $P < 0.0001$) than the other host species, resulting in a difference in cowbird egg distribution among 50 nests of the same 6 host species listed above and between years 1980 and 1981 (Mann-Whitney U -test, $P = 0.0075$). The high rate of parasitism in 1980 had a detrimental effect on cowbird reproduction as indicated by the number of juvenile cowbirds trapped during June and July of 1980 (0) compared to 1981 (40; Wilcoxon's signed-ranks test, $P < 0.01$).

Altamira Orioles (*Icterus gularis*) escaped parasitism. During 15 minutes of observation at each oriole nest, I saw female cowbirds enter 4 of the 24 nests. Although we visually inspected only 2 of the oriole nests, we found no nestling or fledgling cowbirds with the 24 breeding oriole pairs observed during 1980 and 1981.

We discovered a total of seven Brown-headed Cowbird eggs distributed among six nests of three host species (Table 4). All six nests also contained eggs of the Bronzed Cowbird and four of the nests contained no host eggs. These six nests suffered predation before any eggs hatched.

FEMALE COWBIRD EGG-LAYING AND EGG-PIERCING BEHAVIOR

Female cowbirds continued to add eggs to nests even when the clutch was already large and/or incubation was advanced. The latest egg laid, as measured by its hatching date relative to nestmates, hatched in a thrasher nest five days after the youngest nestmate in the brood. The largest incubated clutches were hosted by

TABLE 3. The distribution of Bronzed Cowbird eggs and/or young among nests discovered in 1980 (a) and 1981 (b).

Species	Year	Number cowbird eggs or young per nest*								Total nests
		0	1	2	3	4	5	6	7	
Green Jay	a	—	1	2	1	—	1	1	—	6
	b	—	3	—	1	1	—	—	1	6
Long-billed Thrasher	a	—	5	6	2	—	1	—	—	14
	b	1	2	4	2	—	1	1	1	12
N. Mockingbird	a	—	4	2	6	—	2	2	—	16
	b	10	7	2	—	—	—	—	—	19
Red-winged Blackbird	a	—	1	—	—	—	—	—	—	1
	b	1	1	1	—	—	—	—	—	3
N. Cardinal	a	—	4	—	1	—	—	—	—	5
	b	—	1	2	—	—	1	—	1	5
Olive Sparrow	a	—	3	1	1	—	1	—	—	6
	b	—	1	2	—	—	1	—	1	5
Groove-billed Ani	a	9	—	—	—	—	—	—	—	9
	b	3	—	—	—	—	—	—	—	3
Yellow-billed Cuckoo	a	14	—	—	—	—	—	—	—	14
	b	13	—	—	—	—	—	—	—	13
Couch's Kingbird	a	10	1	—	—	—	—	—	—	11
	b	8	—	—	—	—	—	—	—	8
Cactus Wren	a	5	—	—	—	—	—	—	—	5
	b	1	—	—	—	—	—	—	—	1
Verdin	a	1	—	—	—	—	—	—	—	1
	b	1	—	—	—	—	—	—	—	1
Altamira Oriole	a	11	—	—	—	—	—	—	—	11
	b	13	—	—	—	—	—	—	—	13
Curve-billed Thrasher	a	9	—	—	—	—	—	—	—	9
	b	11	—	—	—	—	—	—	—	11
Great-tailed Grackle	a	—	—	—	—	—	—	—	—	0
	b	4	—	—	—	—	—	—	—	4

* This table excludes eggs found in two dump nests.

Green Jays (11 eggs, 7 of which were cowbird) and a Long-billed Thrasher (10 eggs, 7 of which were cowbird).

Of 14 nests that I inspected once every 24 hr, 10 (71%) of them contained a single pierced host egg or cowbird egg following their parasitism by a cowbird. The other 4 nests contained no pierced eggs. Of the eggs in 22 parasitized nests that contained pierced eggs, about twice as many host eggs (67%) were pierced compared to those of the cowbirds (32%; Table 5). Final host clutch sizes (Table 6) were lower than expected for all six host species. Host egg

TABLE 4. Bronzed and Brown-headed cowbird egg distribution among nests of the three host species parasitized by the Brown-headed Cowbird at SANWR 1980–1982.

Host species	Host	Number of eggs	
		Bronzed Cowbird	Brown-headed Cowbird
Mockingbird	1	5	1
Cardinal	1	1	1
Cardinal	0	3	1
Olive Sparrow	0	1	1
Olive Sparrow	0	2	1
Olive Sparrow	0	0	2 ^a
Totals		12	7

^a Both eggs laid on same day.

number was most reduced, relative to other hosts, in Olive Sparrow (78%) and cardinal (91%) clutches, and least reduced in Red-winged Blackbird (33%) clutches. The host-to-cowbird fledgling ratios for the nests in which cowbird nestling measurements were made in 1980 (Table 7) indicate that the reproductive efforts of pairs of several species were devoted entirely to raising cowbirds. Additionally, several cowbirds were able to successfully coexist in (and fledge from) the same nest.

We found 12 cases (Green Jays, 3; Long-billed Thrashers, 2; mockingbirds, 4; cardinals, 1; Olive Sparrows, 2) of multiple same-day parasitism. As many as 5 cowbird eggs were added within a 24-hr period to nests of these hosts. Each instance represents a case of more than one female laying in the same nest.

FEMALE GROUPS

Female cowbirds travel alone or in groups of two to six while searching for nests. At least once during each daily observation period, we noted females converging to a location from several different directions. The focus of this behavior was invariably other female cowbirds, a calling bird, or a commotion involving host species. Even though as many as five cow-

TABLE 5. Numbers of pierced eggs in the nests of six host species during 1980 and 1981.

Species	No. of parasitized nests checked	A		B	
		No. nests with pierced host eggs present	No. host eggs pierced of total host eggs present in A	No. nests with pierced cowbird eggs	No. cowbird eggs pierced of total cowbird eggs present in B
N. Mockingbird	16	9	16/24	4	4/27
Long-billed Thrasher	20	1	2/4	2	3/6
Green Jay	5	1	1/1	0	0
Red-winged Blackbird	2	0	0	0	0
Cardinal	3	2	3/4	3	3/8
Olive Sparrow	6	0	0	0	0
Totals	52	13	22/33	9	13/41
Percent			67%		32%

bird eggs appeared in a single nest within a 24-hr period, we never saw cowbirds in groups during dawn hours, the time during which they lay their eggs.

COWBIRD EGGS AND NESTLINGS

I visited four nests (thrasher, $n = 1$; mockingbird, $n = 2$; cardinal, $n = 1$), each of which contained one cowbird egg, on a daily basis from the time eggs were laid until they hatched. The incubation periods were 10, 11, 11, and 12 days. Bronzed Cowbirds were silent during their day of hatching, but the next day they began to gape and vocalize while same-aged host nestmates were silent.

Cowbirds that hatched 48 hr or more after nestmates did not survive ($n = 10$) regardless of host species. In contrast, of the cowbirds that hatched 1 to 36 hr later than nestmates, 60% ($n = 5$) fledged; and of the cowbirds that hatched in synchrony with or before nest-

mates, 77% ($n = 13$) fledged. All three of the cowbirds reared as lone nestlings successfully fledged.

All of the Bronzed Cowbird nestlings that we handled or observed ($n = 65$) had red mouth linings and cream-colored mouth flanges. Similarly, the cowbird eggs ($n = 166$) showed little variation in size and color. Although egg size and color were not measured, all eggs were pale blue and unmarked.

The single hatching-year Brown-headed Cowbird that I observed (and collected) had yellow flanges and pink mouth lining. It was being fed out of the nest by Olive Sparrows, and was apparently raised in the same nest as a Bronzed Cowbird that was being fed by the same adults.

Among the refuge host species, only the Long-billed Thrasher, Red-winged Blackbird, and Northern Cardinal nestlings had mouth and flange coloration like that of the Bronzed

TABLE 6. Average final host clutch size (FCS) for parasitized and unparasitized nests, the average number of cowbird eggs per parasitized nest, and the ratio of host to cowbird eggs in parasitized nests for six host species, showing clutch reduction (%) due to parasitism.

Species	Ave. FCS for unparasitized nests	Ave. FCS for parasitized nests	% Reduction	Ave. no. cowbird eggs in parasitized nests	Ratio of eggs host : cowbird in parasitized nests
Green Jay	4.0 ^a	1.8 $n = 5$ SE = 0.58	55%	4.4 $n = 5$ SE = 1.08	1:2.4
Long-billed Thrasher	3.76 $n = 3$ SE = 0.33	1.78 $n = 18$ SE = 0.22	53%	3.1 $n = 18$ SE = 0.50	1:1.8
Mockingbird	3.8 $n = 11$ SE = 0.12	1.5 $n = 16$ SE = 0.34	61%	2.4 $n = 16$ SE = 0.36	1:1.6
Cardinal	3.5 ^b —	0.3 $n = 3$ SE = 0.33	91%	2.76 $n = 3$ SE = 0.88	1:8.1
Olive Sparrow	4.0 $n = 1$ —	0.9 $n = 7$ SE = 0.58	78%	1.86 $n = 7$ SE = 0.63	1:2.1
Red-winged Blackbird	3.0 $n = 2$ SE = 1.0	2.0 $n = 2$ SE = 1.0	33%	1.0 $n = 2$ SE = 0	2:1

^a From Bent (1964).

^b From Bent (1968).

TABLE 7. The ratio of cowbird to host young that fledged from thirteen parasitized nests.

Foster species	Fledgling ratio (host: cowbird)	No. of nests
N. Mockingbird	0:3	2
	0:2	1
	0:1	2
Long-billed Thrasher	1:3	1
	2:2	2
	1:2	1
	0:1	1
	3:1	1
Green Jay	0:3	1
Couch's Kingbird	0:1	1

Cowbird. In contrast, Northern Mockingbirds ($n = 38$) had cream-colored flanges and yellow mouth linings, and the Olive Sparrow nestlings ($n = 3$) had mouth coloration similar to that of the Brown-headed Cowbird.

The unmarked Olive Sparrow eggs ($n = 13$) ranged in color from white to pale pink. The eggs of all other hosts were marked and could be distinguished on that basis from eggs of the Bronze Cowbird.

The sexual size dimorphism that I found when measuring adult cowbirds ($n = 364$; Table 8) was also evident for hatching-year cowbirds. In addition to plumage differences between adult males and females, weight (males, $\bar{x} = 68.94$ g; females, $\bar{x} = 56.93$ g) and wing cord (males, $\bar{x} = 117.21$ mm; females, $\bar{x} = 102.51$ mm) were also reliable indicators of

sex. I noted similar size dimorphism between male and female juveniles ($n = 147$) and fledglings ($n = 113$). By dissection, I verified the sex (as determined by weight) of 12 known-age nestlings in addition to all hatching-year individuals that were killed for determination of stomach content (diet; Table 9). Additional confirmation of sex identification based on size came from the recovery of yearlings ($n = 17$) that had been banded during their hatching year.

The cowbird growth rates were similar to those of non-parasitic relatives (Table 8). By the day after hatching, the weights of males and females began to diverge towards the weights of the dimorphic adults. Bronzed Cowbirds fledged at day 10 ($n = 1$), 11 ($n = 7$), or 12 ($n = 6$) after hatching. By fledging age, there were two clearly discrete cowbird weight groups, both approaching 70% of the adult weights (Fig. 3).

DIET

The percent of plant food items (Table 9) differed significantly among the fledgling groups (Kruskal-Wallis one-way ANOVA, $P = 0.006$) being raised by Green Jays, Long-billed Thrashers, or Olive Sparrows. The difference was due to the absence of Texas persimmons (*Diospyros texana*) from the cowbird diet provided by Olive Sparrows. Whereas nestling cowbirds received no plant material in their diet, fledglings were fed diets consisting of as much as 54.1% vegetable matter. Once inde-

TABLE 8. Nestling growth (K , t_{10-90} , and A from Ricklefs, 1967) in relation to weight of adults of five icterid species and of five host species at the study site.

Hosts	Weight of hatchlings (SD)	n	Growth rate (K)	t_{10-90}	A	Weight of adult (SD)	n
Green Jay ^b	—	—	—	—	60.5	78.6 (6.07)	61
Long-billed Thrasher	5.90 (0.42)	6	0.534	8.2	46.0	67.2 ^a (4.64)	17
N. Mockingbird	4.90 (0.77)	7	0.525	8.4	39.0	47.3 ^a (1.25)	9
N. Cardinal	4.70	1	0.415	10.6	36.0	40.0 ^a (4.68)	21
Olive Sparrow ^c	—	—	—	—	20.7	26.9 (3.01)	17
Icterids							
Bronzed Cowbird							
Male	5.12 (1.13)	6	0.493	8.9	47.5	58.9 (4.18)	144
Female	4.18 (0.39)	8	0.472	9.3	38.0	56.9 (5.09)	220
Shiny Cowbird ^d	—	—	0.544	9.3	—	—	—
Brown-headed Cowbird ^e	—	—	0.576	7.6	33.5	43.5	—
Red-winged Blackbird ^f							
Male	—	—	0.536	8.2	48.5	63.0	—
Female	—	—	0.496	8.9	33.1	43.0	—
Yellow-headed Blackbird							
Both sexes ^g	—	—	0.428	10.3	57.0	74.0	—
Female ^h	—	—	0.540	8.1	41.6	54.0	—

^a Data from Bruce A. Fall.

^b Data from Doug Gayou.

^c Data on adults taken from specimens at Bell Museum of Natural History, Univ. of Minnesota.

^d Data from J. R. King (1973a), Argentina.

^e Data from Norris (1947), Pennsylvania.

^f From Ricklefs (1968), Ohio.

^g From Fautin (1941), Utah.

^h From Willson (1966), Washington.

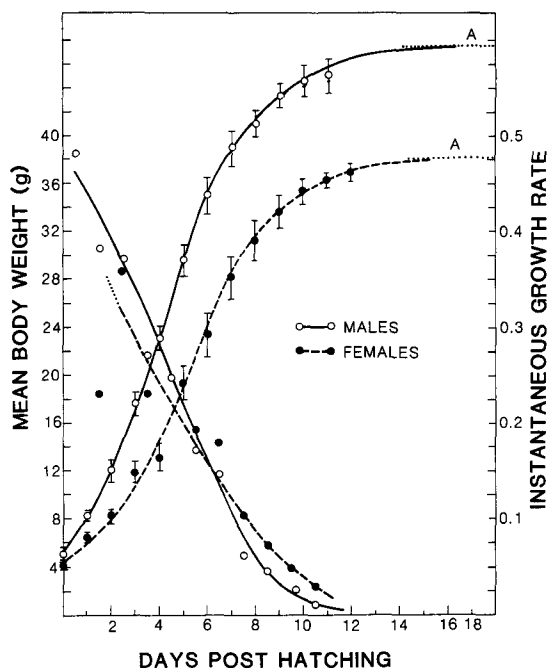


FIGURE 3. Growth curves and instantaneous growth rates for male and female nestling Bronzed Cowbirds (± 1 SE) and the asymptote (A) weight approached by nestlings before fledging.

pendent, juveniles ate a variety of seed types accounting for over 76% of their food intake.

RELATIVE SUCCESS OF FOSTER PARENTS

Table 10 shows each host species' relative success (weighted by their abundance) at rearing cowbirds. The larger host species (Green Jays

and Long-billed Thrashers) were the most successful among those censused (Chi-square test, $P < 0.005$), while Olive Sparrows were the least successful, based on total number of cowbirds produced. None of the seven species that used domed or cavity nests were seen feeding fledgling cowbirds.

HOST'S COUNTER-ADAPTATIONS TO PARASITISM

Of the experimental (real) cowbird eggs that were placed in four nests of each of three species (Couch's Kingbirds, Curve-billed Thrashers, and Great-tailed Grackles), all were ejected within 48 hr. Additionally, Couch's Kingbirds aggressively chased other bird species, including cowbirds, from the vicinity of their nests. Similarly, Northern Mockingbirds (1 observation) and Red-winged Blackbirds (1 observation) fought with cowbirds and often flew towards approaching cowbirds. In contrast, Green Jays, Long-billed Thrashers, Northern Cardinals, and Olive Sparrows did not appear to be aggressive towards avian intruders, including cowbirds, at any time.

DISCUSSION

COWBIRD NUMBERS AND BREEDINGS SYNCHRONY WITH HOSTS: EFFECTS ON REPRODUCTIVE SUCCESS

Cowbirds did not arrive at the study site until mid-April in all three years. The first cowbird eggs were found in the first week of May in 1980 through 1982, regardless of possible earlier host breeding activity. For Bronzed Cow-

TABLE 9. Average percent of identifiable food items in stomachs of hatching-year Bronzed Cowbirds collected during June-August, 1982.

	Juveniles (<i>n</i> = 12)	Fledglings dependent on:			Nestlings ^d
		Long-billed Thrasher (<i>n</i> = 37)	Green Jay (<i>n</i> = 32)	Olive Sparrow (<i>n</i> = 4)	
Milo (<i>Sorghum</i>)	23.5 (4) ^a	—	—	—	—
Small seeds ^b	30.1 (7)	1.7 (7)	2.1 (6)	2.8 (3)	—
<i>Diospyros texana</i>	11.3 (3)	38.7 (24)	17.3 (10)	—	—
Drupes ^c	11.4 (6)	13.7 (24)	12.5 (17)	9.0 (4)	—
Ave. % seed material (sum rows 1-4)	76.3	54.1	31.9	11.8	—
Gastropods	0.7 (1)	0.8 (16)	1.0 (21)	1.0 (4)	6.3 (3)
Arachnids	—	0.1 (2)	0.6 (9)	0.3 (1)	15.0 (9)
Diplopods	—	0.5 (1)	—	—	—
Orthopterans	0.42 (1)	3.7 (6)	7.8 (10)	1.3 (1)	2.1 (3)
Hemipterans	—	—	0.3 (9)	—	—
Neuropterans	—	0.3 (1)	—	—	—
Hymenopterans	—	0.1 (1)	—	—	—
Lepidopterans	—	0.3 (1)	0.3 (1)	—	—
Vermiform larvae	13.3 (3)	22.2 (18)	9.2 (9)	26.3 (3)	28.8 (10)
Arthropod eggs	—	0.1 (2)	0.1 (4)	0.3 (1)	—
Unidentified insects	9.3 (8)	18.0 (34)	48.8 (29)	59.3 (4)	47.8 (12)

Kruskal-Wallis one-way ANOVA (row 5 among the 3 fledgling groups) $P = 0.006$

^a Numbers in parentheses are the number of individuals of *n* having food items in stomachs.

^b Small seeds include *Sesbania drummondii*, *Panicum* sp., *Setaria* sp., *Amaranthus* sp.

^c Drupes include *Condalia hookeri*, *Celtis pallida*, *Bumelia angustifolia*.

^d Of the 12 nestlings, 11 were in Long-billed Thrasher nests and one was in a mockingbird nest.

TABLE 10. Dependent fledging Bronzed Cowbirds recorded for each host species seen feeding cowbird fledglings in 1981 and 1982.

Host species	Relative abundance	1981		1982	
		Observed	Expected	Observed	Expected
Green Jay	0.1335	14	7.209	41	13.2165
Long-billed Thrasher	0.3535	24	19.089	48	34.9965
Red-winged Blackbird	0.0115	2	0.62	—	1.1385
Cardinal	0.0458	2	2.4732	1	4.5342
Olive Sparrow	0.4557	12	24.6078	9	45.5342

Chi-square test, $df = 4$, $P < 0.005$.

birds, known to be "late breeders" (Friedmann 1929), and other generalist brood parasites, the onset of reproduction probably coincides with the average of initial egg-laying dates for many of their local hosts.

A drought during the spring of 1980 probably delayed the onset of reproduction for all host species until late April or early May. This resulted in strong synchrony of host and cowbird breeding seasons and intense (100%) parasitism of the regular hosts. The detrimental effect of such intense parasitism on host reproduction is indicated by the numbers of juvenile cowbirds trapped in 1980 compared to 1980 (0 to 40). The difference in the number of juveniles trapped during June and July in 1980 versus 1981 reflects different reproductive success between years rather than delayed cowbird reproduction in the former year. The avian reproductive success at the study site in 1980 was probably a result of drought-related effects.

Hosts that are abundant and aggressive in their nest defense (i.e., mockingbirds) and those that nest synchronously with conspecifics or before cowbirds come into reproductive condition may experience reduced parasitism (Clark and Robertson 1979). However, aggressive behavior by hosts towards Bronzed Cowbirds may be effective only when the number of cowbirds is low. I interpret the difference in rate of parasitism of mockingbirds in different years to be primarily (1) the result of a decrease in Bronzed Cowbird numbers at the SANWR in 1981 and (2) the effect that cowbird abundance had on overcoming aggressive mockingbird nest defense in 1980. I conclude that it may be easier for large numbers of gregarious female cowbirds to gain access to nests of the most defensive host species. However, as access becomes easier and rates of parasitism increase, the reproductive success of cowbirds and hosts may decrease due to greater intra- and interspecific nestling competition, predation effects, and other factors. Therefore, I agree with other authors (McGeen 1972, Lown 1980) that there is probably an abundance level of parasites above which cowbird success decreases.

ADAPTATIONS AND COUNTER-ADAPTATIONS TO PARASITISM

Individual cowbirds were probably drawn to the same nest by various cues resulting in group formation. Threatened hosts often vocalized; some resulting calls may have given clues to nest-searching female parasites. A group of cowbirds, taking advantage of the increased commotion that a prospective host faces from more than one intruder, may be more likely to gain nest information than would any of them alone. It is possible that all members of a group could successfully lay in the same nest on the same day. In this light, the behavior of individual members of a group should be interpreted as coincidentally mutualistic.

In response to cowbird intrusion, is strong nest defense by suitable hosts adaptive behavior? Such defensive behavior appears to be maladaptive when host population size is low and when it draws increased cowbird attention to nest location (Robertson and Norman 1977, Clark and Robertson 1979). This would be true especially for hosts encountering abundant, gregarious parasites like the Bronzed Cowbird in south Texas (this study). In addition to gaining nest location information, parasites may use host reaction to cowbird intrusion as a clue to the age and experience of prospective hosts. J.N.M. Smith et al. (1984) present evidence for selective parasitism of Song Sparrows (*Melospiza melodia*) by Brown-headed Cowbirds. Yearling female sparrows were less parasitized than older, more experienced ones. Even if maladaptive, such defense behavior may occur as part of a generalized response to potential enemies, including parasites and predators.

Host susceptibility to parasitism is affected by many factors in addition to the host's overt behavior to preclude parasitism. Other factors include the abundance of non-territorial parasites (McGeen 1972), colony size for colonial nesters (Clark and Robertson 1979), the degree of host-parasite breeding synchrony (McGeen 1971, Middleton 1977, Anderson and Ohmart 1978, this study), the degree to which parasites select particular hosts (Post and Wiley 1976,

1977; J.N.M. Smith et al. 1984), the degree of nest concealment (Rothstein 1975a), and other community factors (Elliot 1976, Lowther and Johnson 1977). Rejection of foreign eggs by hosts is classified among the overt behavior patterns evolved to reduce the risks of parasitism.

Evidence for parasitism of rejector species has been provided and discussed by several researchers (Rothstein 1971, 1976; Friedmann et al. 1977). However, I could not determine the degree to which the three ejector species identified here were naturally parasitized. I did not find any cowbird eggs in active nests of Great-tailed Grackles or Curve-billed Thrashers and only a single parasite egg in one Couch's Kingbird nest (of 19). The rate of parasitism for the Kingbird would be as low as observed (about 5%) only if cowbirds have some way of assessing the behavior of individual hosts to identify the minority that are accepters and then laying eggs in those nests only. Because cowbird egg placement is often indiscriminate, such assessment by cowbirds is unlikely. Although only one kingbird nest was successfully parasitized, it is possible that the rate of parasitism for the kingbird is high, with the vast majority of cowbird eggs being ejected. This is only the fifth reported case of parasitism for this species, and my record of a cowbird fledged from the nest is the first for this species. If no more than 5% of all kingbirds are accepters (probably a reasonable assumption; see Rothstein 1975b) and if cowbirds do not discriminate against kingbird nests, this host is a poor choice for parasitism and illustrates wasteful laying behavior by the cowbirds. On the other hand, kingbirds may represent a better choice for cowbirds than certain other rejector species (i.e., Cedar Waxwings, *Bombycilla cedrorum*; Rothstein 1976) whose diets are unacceptable to nestling cowbirds.

EFFECTS OF EGG PIERCING

Female Bronzed Cowbirds usually pierce one egg prior to laying their own. As in Mason's (1980) study of Shiny Cowbirds (*M. bonariensis*), I found that Bronzed Cowbirds pierced more host eggs (67%) than cowbird eggs (32%). The frequency of egg piercing may provide a clue to individual laying behavior. If a cowbird can distinguish host from parasitic eggs, before laying her first egg in a nest she should pierce cowbird eggs, if present, because they represent the greatest competitors to her egg (Mason 1980). If the same female lays a second egg in a previously parasitized nest, she should destroy host eggs if she cannot distinguish her eggs from those of conspecifics. All Bronzed Cowbird eggs in our study were pale blue and

unmarked. Of all SANWR hosts, only Olive Sparrow eggs were unmarked, but they were pale pink or white in color. Assuming that cowbirds can distinguish cowbird eggs from host eggs but cannot discriminate between their own and other cowbird eggs, the relative percentages of pierced cowbird eggs should reflect the frequency of multiple hen parasitism of those nests. The number of pierced host eggs should correlate with multiple parasitism of nests by the same individual. I have no data on individual females laying more than one egg in any nest but, based on my observations of multiple same-day parasitism, I conclude that same-nest parasitism by different females is common, regardless of host size and past success as fosterers.

Egg hatching order and brood size (including parasites) are two determinants of nestling survival (Lack 1954, Ricklefs 1965, Eastzer et al. 1980). However, even before any eggs hatch, the adult female cowbird may reduce competitors to her egg by destroying other eggs, making the time of her egg laying less critical to her young's survival. Egg-piercing behavior by female cowbirds is common, but such behavior may not always be detectable. I interpreted final clutch sizes that were lower than expected as evidence that egg damage had occurred, followed by removal of broken eggs by the hosts. This interpretation is supported by Rothstein (1982).

Olive Sparrow and Northern Cardinal nests sustained the greatest reduction in numbers of their own eggs; they appeared to be the least nest-attentive (most reclusive) among the common hosts. However, even attentive species had broods consisting only of cowbirds. Red-winged Blackbirds had the lowest percent clutch reduction, probably owing to their colonial nature, their aggressive disposition, and the absence of cowbird observation perches in the vicinity of the marshes. Colony size has been shown to be inversely proportional to rates of parasitism (Clark and Robertson 1979). This may be due to nearby blackbirds, which respond to distress calls of their neighbors, resulting in greater cowbird harassment.

EFFECTS OF HOST SPECIES SIZE AND PREDATION

Because most passerines primarily feed arthropods to their young, few species of that order should be unacceptable as hosts (Hamilton and Orians 1965, Skutch 1976) for nutritional reasons. Differences in diets provided by hosts in our study may be attributed to the feeding of Texas persimmons by the larger host species to their young. These fruits are prob-

ably too large for the smaller hosts to manage. A persimmon drupe can occupy a large portion of the stomach and may take longer to digest or be eliminated than softer items, resulting in an uncorrected bias. Dietary differences among hosts due to size disparity probably has little effect on their success as fosterers.

Fretwell (cited by Rothstein 1975a) suggested that cowbirds should prefer large hosts over small because of their superior nest defense and ability to care for larger broods. Alternatively, the cowbirds could show a preference for large hosts with large nests that are easier to find than those of smaller hosts (Rothstein 1975a). Shiny, Brown-headed, and Bronzed cowbirds repeatedly parasitize individual nests of both large and small passerine hosts over all or parts of their respective ranges (Friedmann 1929; McGeen 1971, 1972; Lowther 1977; Elliot 1977, 1978; Mason 1980; this study). Mason (1980) found that host reproductive efforts correlate well with host body size, explaining why Shiny Cowbirds preferred large hosts whose nests they parasitized repeatedly. In analyzing Rothstein's (1975a) data on ejector species, Mason concluded that the Brown-headed Cowbird may have been forced to parasitize smaller hosts when heavily parasitized larger hosts became ejectors.

Larger hosts, including thrashers and jays, may be better nest defenders against predators (Gottfried 1979) accounting for their success, compared to other host species, in south Texas, in rearing young cowbirds (this study). Nest defense may be especially important if nestlings are likely to draw increased predator attention to a nest (Friedmann 1929, Snow 1962). Crypticity of nests may lessen the degree of parasitism and predator detection before any eggs hatch. However, once cowbird hatchlings begin their incessant begging, some of the benefits of nest concealment are lost and nest defense may then become more important to nestling survival. Alternatively, because nests of these more successful hosts may not be easily accessible to non-climbing predators, they may face fewer dangers than nests placed closer to the ground.

Terrestrial mammals at the SANWR (e.g., coyotes, *Canis latrans*; striped skunks, *Mephitis mephitis*; and bobcats, *Lynx rufus*) may be important predators on birds' nests. For nests located near ground level, predation rates should be greater for heavily parasitized nests compared to those containing fewer conspicuous nestlings (Gochfeld 1979) or those at a greater height. Nests containing more than one cowbird nestling should be especially attractive to predators using auditory location clues. For that reason, selection should favor cow-

birds laying one egg per nest (Payne 1977a) to maximize their chances of breeding success. However, I suggest that two eggs laid by one cowbird in the nest of a thrasher or jay, despite the nestling size disparity, could be a better egg investment than one egg laid in two different nests of species more prone to predation due to presence of cowbird nestlings.

BRONZED COWBIRDS AS NESTLINGS

Like the young Shiny (Gochfeld 1979) and Brown-headed cowbirds (Eastzer et al. 1980), Bronzed Cowbird nestlings possess no apparent morphological adaptations for parasitism. However, Bronzed (this study), Shiny (Gochfeld 1979), and Brown-headed cowbirds (Friedmann 1929) are excellent competitors as nestlings, probably due to their vocal nature relative to most host nestmates. More data are needed on begging rates of the cowbirds and non-parasitic close relatives to evaluate this behavior as a possible adaptation or preadaptation for parasitism. The time required for incubation and the rate of growth of nestlings are similar to those of host species measured here and parasitic and non-parasitic close relatives. My estimate of the Bronzed Cowbird overall growth-rate constant (K) is lower than that reported for the smaller Shiny and Brown-headed cowbirds. Perhaps unexpectedly, male Red-winged Blackbirds and Bronzed Cowbirds grow faster than conspecific females despite the larger size of males. Northern Mockingbirds, Long-billed Thrashers, Red-winged Blackbirds, and Northern Cardinals have K s comparable to that of the Bronzed Cowbird (0.415 to 0.534). My values fell within the theoretical range for subtropical species (0.40 to 0.52, Ricklefs 1969).

SOME BENEFITS AND COSTS OF GENERALIST BEHAVIOR

Optimization (as used by J. M. Smith 1978 and by Lewontin 1978a, 1978b) of egg-laying behavior by female cowbirds probably involves a compromise between selection pressures acting to maximize egg survival, such as appropriate nest choice, and those acting to maximize egg production. The benefits of parasitizing unfamiliar hosts must be greater than the costs (increased exposure to predators while foraging and energy content of an egg, among others), even if some inappropriate choices are made.

Many brood parasites produce relatively small and therefore energetically inexpensive eggs (J. R. King 1973b, Payne 1974). Ankney and Scott (1980) found that laying female Brown-headed Cowbirds did not draw on fat or protein reserves for egg formation but in-

stead used nutrients and energy from their daily diet. As a result, egg production is not as costly, in energetic terms, as had been thought (Ricklefs 1974). Maximum egg production with some risk taking appears to be the most adaptive course possible. I agree with Rothstein (1976) that some wastage may be an unavoidable cost of the generalist laying pattern.

Dump nests are consequences of risk taking and a lack of familiarity with nest status. Friedmann (1929) and Friedmann et al. (1977:65) stated that wandering yearling Shiny and Bronzed cowbird females without "territories" were probably responsible for dump nesting late in the breeding season. In contrast, Brown-headed Cowbirds are known to dump-nest less frequently than these other two congeners (Friedmann et al. 1977). Dufty (pers. comm.) suggested that dump-nest frequency differences among the cowbird species may be related to differences in social systems. The non-territorial female Bronzed Cowbirds (Carter 1984) and Shiny Cowbirds are more likely to gain access to dump nests than are territorial female Brown-headed Cowbirds. I suggest an alternate explanation that takes into consideration the combined effects of differences in cowbird social systems and ranges. A female cowbird intending to parasitize nests that suffered predation while her egg was forming is forced to find another site quickly. Unfamiliar nests containing eggs may represent her best alternative in the absence of nest status information. Given this, the frequency of dump nesting is a measure of the frequency of predation on host nests at the same time and place. Several researchers have suggested that tropical predation rates exceed those in temperate areas (Skutch 1949, 1954, 1960; Cody 1966; Foster 1974). If true, dump-nest frequency should be higher for tropical parasites (e.g., Shiny and Bronzed cowbirds) compared to those of the temperate zone (e.g. Brown-headed Cowbirds). This prediction is supported by evidence reported by Friedmann et al. (1977: 65).

For brood parasites, egg placement and egg survival are nearly independent events. Emancipation from parental duties allows females to invest a greater fraction of their energy budget in egg production compared to non-parasitic species. Therefore, parasites may be expected to have higher seasonal fecundity (as discussed by Scott and Ankney 1983) than non-parasitic close relatives. I feel that some egg wastage or improper nest choice by the parasites does not necessarily indicate a lack of fine-tuning by the parasites to their hosts or a less evolutionarily-advanced parasitic habit. Rather, it should be viewed within the ecological

context of the generalist reproductive behavior of the parasite, for example, low probability of egg survival due to predation or destruction by conspecifics.

HOST SPECIFICITY AMONG BROOD PARASITES

The disparity in host species lists for the Shiny Cowbird (176), the Brown-headed Cowbird (216), and the Bronzed Cowbird (72, Friedmann et al. 1977, Carter 1984) across their entire ranges may be due to their encountering different numbers of species to parasitize or due to inadequate host data on the Bronzed Cowbird. Alternatively, the Bronzed Cowbirds could be showing a preference for hosts of moderate to large body size, as is suggested by its current host species list. Regardless, egg-laying habits of individual parasites are of particular interest, as natural selection works at that level. Generalizations about the parasitic species as a whole may be misleading and inaccurate.

Although few host species are available to the Bronzed Cowbird at the SANWR and all hosts there except the Olive Sparrow can be considered moderate to large in size, the results of my quantitative analysis of parasitism of all common host species show only that the Bronzed Cowbird population in south Texas is not host specific. However, in the absence of egg mimicry it is difficult to discern exactly what the laying behavior of individual Bronzed Cowbirds is, and my analysis applies only to the population as a whole. If Friedmann's (1929) observations on Bronzed Cowbird host choice in south Texas in the 1920s were a true indication of its parasitic preferences, orioles' nests may have been chosen for parasitism by the cowbirds because of oriole abundance and ease of access due to lack of nest crypticity or nest defense. Regardless, extreme parasitism of particular hosts (even if by all members of a population) over a relatively short time does not necessarily represent a tendency towards permanent specificity, and shifts in host choice should occur as relative host availability changes (Southern 1954, Mayfield 1965). In fact, only a few generations may be required for host selection to change (Friedmann 1968), even for the cuckoo species that show narrow host specificity (Phillips 1948, Lack 1968).

In south Texas, the distributions of several species (including five oriole species) that previously bred on or near the SANWR have been changing over the past four decades (Goldman and Watson 1953; Webster 1957, 1958). The cause of these changes has not been explored, but human-caused habitat perturbation, habitat succession, and cowbird parasitism are

possible factors. At the study site, Altamira Orioles have increased in abundance (refuge manager's narratives) while the Hooded Oriole (*Icterus cucullatus*) is now absent except during migration (pers. obs.). This latter oriole species was thought to have been a favorite host of the Bronzed Cowbird with an estimated SANWR density of 400 pairs in the late 1940s (refuge manager's narratives). Breeding Audubon's (*I. graduacauda*), Orchard (*I. spurius*), and Northern orioles (*I. galbula*) have also disappeared from the refuge although their former abundances are unknown. As the Altamira is the only oriole species whose numbers have increased, it merits special attention. Over two seasons, I inspected only two of the 24 Altamira Oriole nests found; neither had been parasitized. In 1982 I found a broken cowbird egg on the ground directly beneath an oriole nest that had been repeatedly entered by cowbirds but had escaped parasitism. Few cases of parasitism of these orioles have been reported. Of 150 nests inspected by Meitzen (cited by Friedmann 1963), only 2 had been parasitized. Webster (1962) reported that 2 of 13 Altamira Oriole nests had cowbird egg shell fragments in them but no whole eggs, while the other 11 had not been parasitized. These data suggest that the majority of Altamira Orioles, like congeneric Northern Orioles (T. S. Smith 1972; Rothstein 1975a, 1977) may eject foreign eggs.

Despite the fact that not all host species at the SANWR were equally successful as fosterers, the cowbirds distributed their eggs equally among them. This suggests to me that Bronzed Cowbirds do not tend to parasitize their foster-parent species (as predicted for generalists). Similar to what Rothstein (1976) has suggested concerning host usage by Brown-headed Cowbirds, I suggest that Bronzed Cowbirds probably hatch with genetically programmed generalized egg-laying behavior including information about types of nests to seek out or to avoid parasitizing. This would allow them to take advantage of naive host species (lacking counter-adaptations) that their parents did not encounter. This would be especially important for parasites when they cause host extirpation or when they expand their range. It might also partially explain the non-random yet, at times, indiscriminate cowbird egg distribution, often resulting in egg wastage.

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